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The influence of air pollution on moss - dwelling animals: 2. Aquatic fauna with emphasis on Nematoda and Tardigrada

Werner A. STEINER
Swiss Federal Research Station for Arboriculture, Viticulture and Horticulture,
Department of Entomology and Nematology,
CH-8820 Wädenswil, Switzerland.

The influence of air pollution on moss-dwelling animals: 2. Aquatic fauna with emphasis on Nematoda and Tardigrada. - The effects of gaseous air pollutants on the moss-dwelling aquatic fauna were studied along an urban-rural gradient in the region of Zurich (Switzerland). Moss samples from 12 study sites, representing different air quality conditions, were taken in October 1984. Close to 49'000 individuals were extracted. Nematodes and tardigrades were analysed to species level; rotifers were treated as a group. Community structure (species composition and abundance) was related to air pollution. The abundance of nematodes increased with increasing air pollution, while species richness was not significantly affected. In contrast, the number of tardigrade species decreased with increasing levels of SO_2. The abundance of tardigrades and rotifers varied independently of SO_2 and NO_2. Classification and ordination techniques were used to investigate the similarity between samples or study sites based on environmental characteristics, pollution, flora and fauna. Results suggest that air pollution represents an important factor controlling the composition of nematode and tardigrade communities. At the species level, the abundances of four nematodes (*Chiloplectus* cf. *andrassyi*, *Aphelenchoides* sp. 4, *Paratripyla intermedia* and Mononchidae sp.) and two tardigrades (*Macrobiotus persimilis* and *Isohypsibius prosostomus*) were significantly correlated with air pollution. Thus, the aquatic fauna of epilithic moss cushions could serve as an indicator of air pollution.

Key-words: Nematoda - Tardigrada - Moss-invertebrate associations - Community structure - Air pollution - Similarity index - Classification - Ordination - Biological indicator.

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1 INTRODUCTION

The use of simply structured animal communities was advocated by BARRET & KIMMEL (1972) for the evaluation of pollution effects on ecosystems. STEINER (1994) suggests the investigation of moss-dwelling invertebrates as indicators of urban pollution, since this fauna has several desirable properties which an ecological monitoring system should reasonably have. Several studies using moss-dwelling communities show that air pollution adversely affects nematodes (ZULLINI & PERETTI, 1986) and tardigrades (MATHEWS, 1971; SÉMÉRIA 1981, 1982; MEININGER & *al.*, 1985). Pollution influences the moss-dwelling fauna either directly or indirectly through the bryophytes and their associated microflora. Contamination with heavy metals – for example – reduces the abundance of soil-dwelling bacteria, actinomycetes and fungi (BISESSAR, 1982). This may, in turn, cause a reduction in the abundance of bacterial-feeding (SANTOS & *al.*, 1981) and fungal-feeding (BASSUS, 1968; BÅÅTH & *al.*, 1978) nematodes. Since the moss-dwelling fauna is closely related to the fauna of soils, its response to pollution can be used to estimate the risks of exposing soil biota to pollution.

The present paper is part of a detailed study devoted to effects of gaseous air pollutants on the moss-dwelling fauna (see also STEINER, 1995a). It investigates the qualitative and quantitative composition of the moss inhabiting aquatic fauna across an urban-rural gradient (Zurich, Switzerland), and tries to define species associations and/or single species as biological indicators of air pollution. The study of community changes across an urban-rural gradient provides, according to MCDONNEL & PICKETT (1990), the best opportunity to investigate the relative influences of urban and natural environmental factors. Results of the present study, complemented by findings of studies dedicated to long-term dynamics (STEINER, 1995b) and experimental manipulations (STEINER, 1995c), present an overall picture of air pollution effects on the moss-dwelling aquatic fauna.

2 MATERIAL AND METHODS

2.1 SAMPLING PLANS

Four criteria were set up for the selection of the study sites: 1) a minimal number of five moss-grown walls; 2) walls with a W, NW, N, NE or E orientation; 3) known levels of air pollution (SO_2, CO, NO and NO_2); and 4) a weighted number of study sites within each of the three urbanisation categories: urban high traffic, urban low traffic and rural low traffic. Urbanisation categories are defined according to traffic volume (BACHMANN-STEINER & *al.*, 1983) and distance to the center of the city. Complying with these criteria, eight study sites were chosen in the city of Zurich and four in rural areas within the canton of Zurich. Pollution ratings and abbreviations of the study sites are given by STEINER (1994). Concentrations of the four air pollutants differed significantly among urbanisation categories (Kruskal-Wallis test, $p < 0.05$).

A single simultaneous sampling was performed in October 1984 at all study sites. At each site, two moss cushions were selected on each of the five walls according to criteria listed in tab. 1. Four subsamples were taken from each moss cushion and pooled together. The 120 samples were processed according to STEINER (1994). Nematodes and tardigrades were analysed to species level; rotifers were treated as a group. As identification was a time consuming process, species analysis was restricted to the four most heavily polluted roadside sites (urban high traffic) in the city of Zurich and to the four rural sites.

TAB. 1

Criteria used in the survey of natural communities (aquatic fauna) for the standardisation of sampling procedures. The criteria are arranged according to different strata.

Strata Criteria	Standardisation
Moss cushion	
Sampling unit size	1 cm^2
No. of units/moss	4 (= sample)
Thickness	1-2 cm
Minimum cushion size	10 cm^2
Wall	
No. of moss cushions/wall	2
Horizontal distribution of moss	maximum distance
Vertical distribution of moss	up to 1 m above ground
Orientation	W, NW, N, NE or E
Study site	
No. of walls/site	5
No. of study sites	12

2.2 DESCRIPTION OF SAMPLES AND STUDY SITES

For each sample the following qualitative (a) and quantitative (b) variables were recorded: a) type of substrate (sandstone, concrete, limestone); type of wall (sunken wall, freestanding wall, wall of a building); orientation of wall; microclimate (five categories; according to SEAWARD, 1979); moss species; animal species. b) height above sea level; height above ground; pH of the moss cushion; size of the moss cushion; proportion of substrate particles (soil or sand) in the sample; annual mean levels of gaseous air pollutants (SO_2, CO, NO, NO_2); species richness and abundance of the moss-dwelling fauna.

Study sites are described by fauna, flora, air pollutants and environmental characteristics. Thereby, sites are characterised by the occurrence of the qualitative variables mentioned above and by occasion of the following sample characteristics: height above sea level (three classes: ≤ 500 m; 501-600 m; > 600 m); height above ground (three classes: ≤ 50 cm; 51-100 cm; > 100 cm); pH of the moss cushion (three classes: ≤ 6.50; 6.51-7.00; > 7.00); size of the moss cushion (three classes: ≤ 50 cm^2; 51- 250 cm^2; > 250 cm^2); proportion of substrate particles (soil or sand) in the sample (two classes: low; high). All samples of a given study site were expected to have been exposed to the same pollution levels.

2.3 Data analysis

2.3.1 *At the community level*

Statistical tests and classification methods were used to relate community characteristics to air pollution and other environmental factors. The classification of samples (or study sites) was performed with the sample (or study site) by species matrix. To classify the species, the sample by species matrix was transposed, excluding taxa with less than ten individuals as well as samples with less than five individuals.

Similarity and classification of species

A critical step in the classification of ecological communities is the choice of an appropriate measure for quantifying the similarity between samples or species (Wolda, 1981). Due to many zero counts in the data set, similarity indices based on correlation coefficients were inappropriate in the present study.

Schatzmann (1986) suggests measuring the similarity between pairs of species with $\hat{\tau}$, as it has many desirable properties which similarity indices should reasonably be expected to satisfy (Schatzmann & *al.*, 1986). The index $\hat{\tau}$ is an unbiased estimator of the $\hat{\tau}$ index (Van Belle & Ahmad, 1974), which sums up the harmonic means of the true proportions of two species for all habitats. Since in the present account the true proportions of animal species are unknown, $\hat{\tau}$ must be replaced by $\hat{\tau}$. The $\hat{\tau}$ index is composed of $\hat{\tau}_1$ and $\hat{\tau}_2$, which include correction factors that reduce the bias of $\hat{\tau}$. The equations of $\hat{\tau}_1$, $\hat{\tau}_2$ and $\hat{\tau}$, according to Schatzmann (1986), are given below:

$$\hat{\tau}_1 = 2\,\Sigma_i \frac{p_i \; q_i}{p_i + q_i - \dfrac{N_x + N_y}{2\,N_x\,N_y}} \qquad [1]$$

$$\hat{\tau}_2 = 2 - \Sigma_i \left[\left(\frac{1}{p_i} + \frac{q_1\,(N_x - 1)}{p_i\,(x_i - 1)} \right)^{-1} + \left(\frac{1}{q_i} + \frac{p_1\,(N_y - 1)}{q_i\,(y_i - 1)} \right)^{-1} \right] \qquad [2]$$

$$\hat{\tau} = \frac{2\,\hat{\tau}_1}{2 - \hat{\tau}_2 + \hat{\tau}_1};\; 0 \le \hat{\tau} \le 2 \qquad [3]$$

where p_i and q_i are the proportions of species X and Y in habitat i; x_i and y_i are the number of individuals of species X and Y in habitat i, with $\sum_i p_i = 1$; $\sum_i q_i = 1$; $N_x = \sum_i x_i$ and $N_y = \sum y_i$.

For comparison, the similarity between pairs of species was also measured with the PS index (RENKONEN, 1938). Results were basically the same (unpublished). Since the PS index depends heavily on sample size (SCHATZMANN, 1986), the $\hat{\tau}$ index was given preference in the present study.

The similarity coefficients ($\hat{\tau}$) between all pairs of species were arranged in new data arrays in a table termed primary similarity matrix. Description of community structure was approached by the classification of species, i.e. recognition of species assemblages with similar distribution within the samples. A complete linkage clustering was performed with the primary similarity matrix, also represented graphically as a tree diagram. The matrix was then rearranged according to the species sequence in the dendrogram to bring similar species to each other. Under certain circumstances, complete linkage clustering might lead to misclassifications due to strongly dilated distances (PIELOU, 1977). Therefore, all dendrograms were controlled for misclassified items, which are characterised by isolated high coefficients located far from the diagonal in the rearranged similarity matrix. In these cases resulting clusters were corrected according to $\hat{\tau}$ values in the underlying similarity matrix.

Similarity and classificatlon of samples and study sites

Description of "habitat" structure was approached by distinction of samples with similar faunal composition using both nonmetric multi-dimensional scaling (NMDS) and classification (complete linkage clustering). According to LUDWIG & REYNOLDS (1988), NMDS is appropriate if the individual species-abundance pattern can't be expected apriori to be linear. With NMDS a two-dimensional similarity map can be obtained, representing each sample as a point. The distances between all pairs of points reflect as closely as possible the measured faunal similarity of the corresponding samples. Groups revealed by classification and corrected for obviously misclassified samples (see above) were incorporated in the similarity map. Thereby, a reasonable number of groups was obtained by visual examination of the dendrogram.

Classification of sites was performed with the same methods outlined above for the classification of species. In addition to faunal classification, sites were classified according to similarity in flora (species composition), air pollution and environmental characteristics (see chapter 2.2).

2.3.2 *At the species level*

Four approaches were used to search for single indicator species: a) graphical representation of the species composition in groups of classified samples; b) comparison of the distribution of moss-dwelling taxa between urban and rural sites (Mann-Whitney U-test); c) graphical representation (star diagram) of selected nematode and tardigrade taxa in a two dimensional pollution gradient; and d) Spearman-rank correlation to test the relation between faunal characteristics and both SO_2 and NO_2.

3 RESULTS

A total of 6'052 rotifers, 31'404 nematodes and 11'342 tardigrades was recorded in the 120 samples of the faunistic survey. At the eight study sites where species analysis was performed, about 28'000 nematodes and tardigrades were encountered, representing 47 nematode and 13 tardigrade species. Detailed information on species composition is given by STEINER (1994).

3.1 COMMUNITY CHARACTERISTICS

Species richness of tardigrades showed a decreasing trend with increasing SO_2 pollution (tab. 2), whereas species richness of nematodes was not significantly affected. Maximum species number was recorded for nematodes and tardigrades from the rural sites "M" and "H", respectively, while minimum species number was found for tardigrades at the urban sites "T" and "R", and for nematodes at the urban site "W" (fig. 1). Tardigrades were generally represented by less than 50% of the species richness of nematodes.

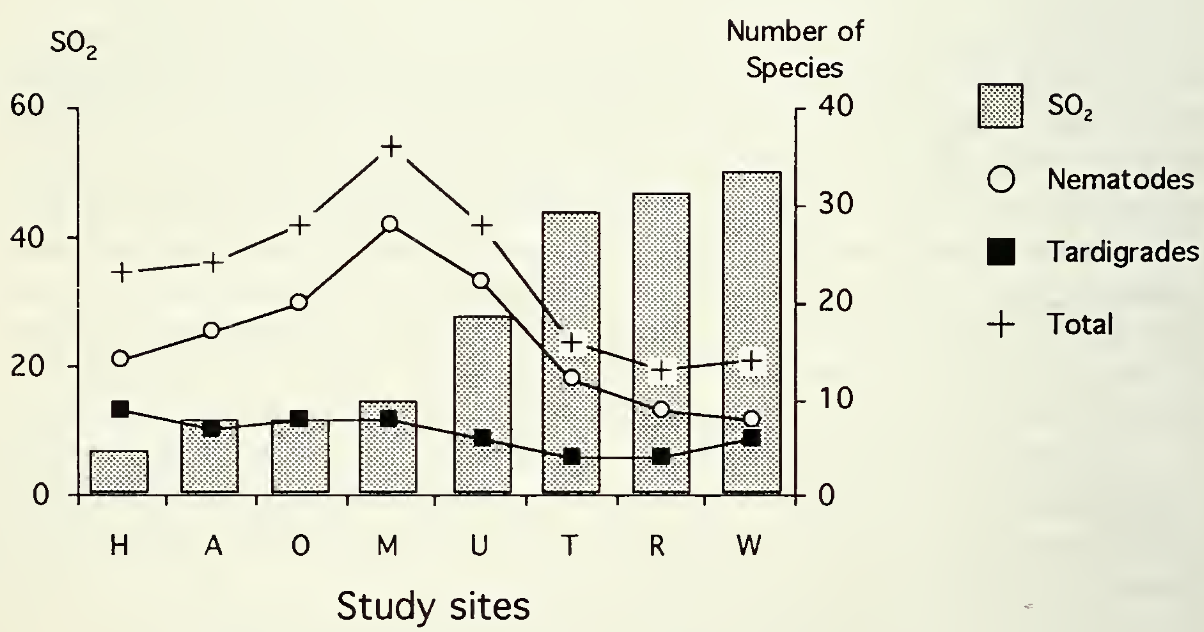

FIG. 1

Species richness (number of species/site) of moss-dwelling nematodes and tardigrades. Study sites are ranked according to annual mean levels of SO_2 ($\mu g/m^3$). Abbreviations for study sites as well as values of SO_2 levels are explained by STEINER (1994). H, A, O and M = rural low traffic sites; U, T, R and W = urban high traffic sites.

TAB. 2

Correlation of community characteristics with annual mean levels of SO_2 and NO_2 (SO_2 and NO_2 in µg/m^3; r_s: Spearman rank correlation coefficient corrected for ties; p: tied probability).

Taxa Community characteristics	No. of sites	r_s	p
Nematodes - SO_2			
Individuals/site (median)	12	+ 0.73	0.016
Tardigrades - SO_2			
Taxa/site	8	- 0.84	0.027
Nematodes - NO_2			
Individuals/site (median)	12	+ 0.59	0.049

Nematodes usually reached larger populations than rotifers or tardigrades (fig. 2). While nematode populations increased significantly with increasing air pollution (tab. 2), the number of tardigrades and rotifers varied independently of SO_2 and NO_2 levels. At the urban sites "T", "W" and "R", the high abundance of some resistant nematode species (fig. 2), together with low species richness (fig. 1) denotes an impoverished fauna.

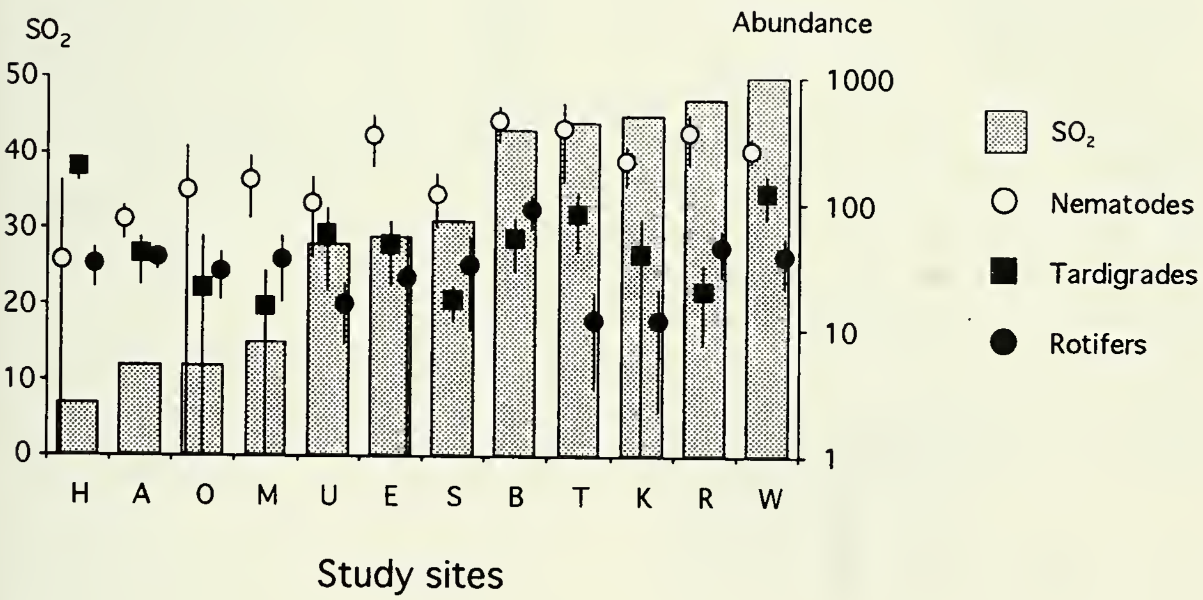

FIG. 2

Abundance (median ± standard error of median) of moss-dwelling nematodes, tardigrades and rotifers (log scale). Study sites are ranked according to annual mean levels of SO_2 (µg/m^3). Abbreviations for study sites as well as values of SO_2 levels are explained by STEINER (1994). H, A, O and M = rural low traffic sites; E, S, B and K = urban low traffic sites; U, T, R and W = urban high traffic sites.

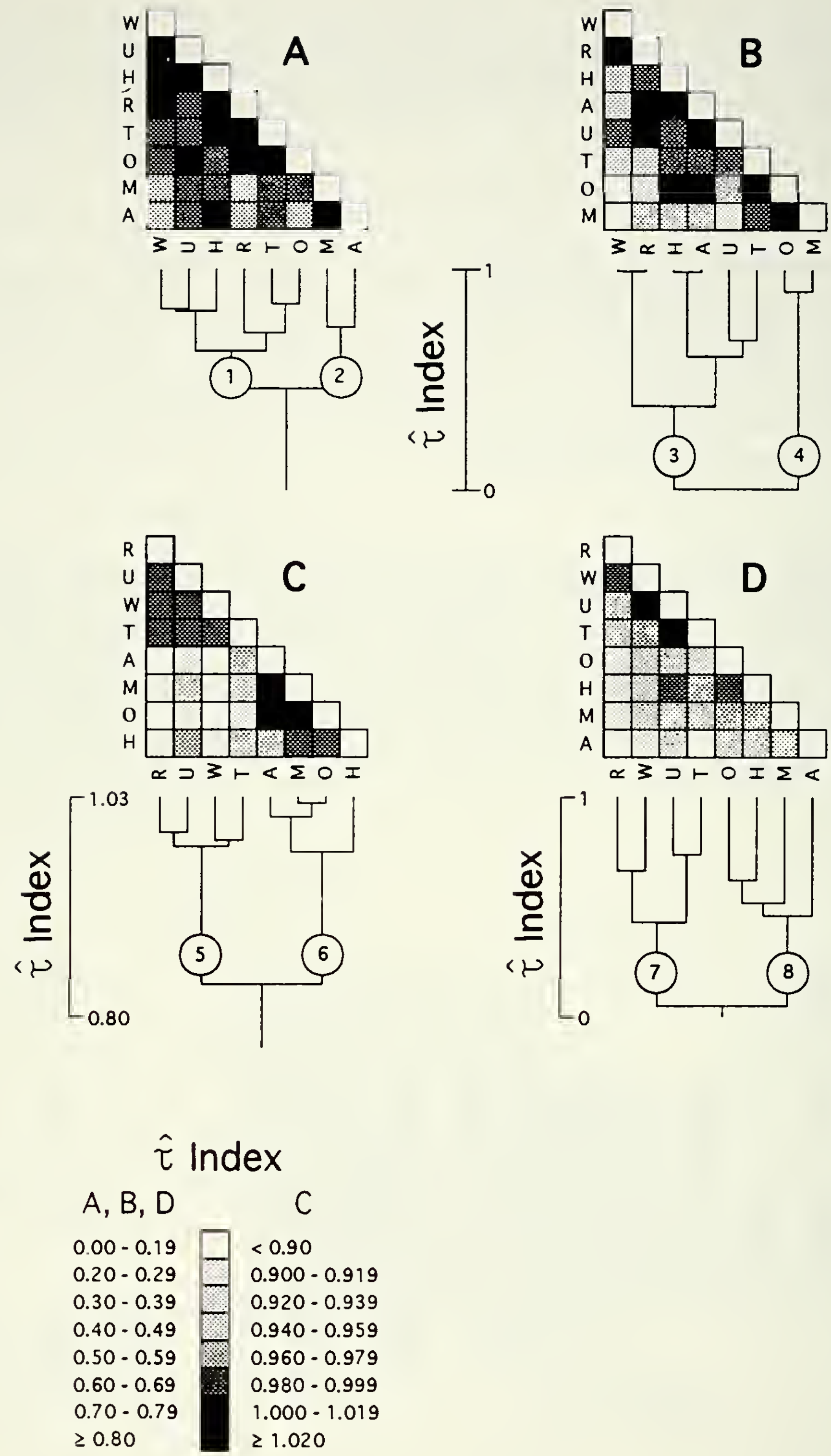

FIG. 3

Similarity matrix and dendrogram representing inter-site relationships in the survey of natural communities. Study sites are characterised by environmental characteristics (A), moss species (B), annual mean levels of SO_2, CO, NO and NO_2 (C) and nematode and tardigrade taxa (D). The similarity coefficients τ are replaced by a shaded grid and rearranged by complete linkage cluster analysis to bring similar study sites to each other. Indicated clusters are discussed in the text. A, H, M and O = rural low traffic sites; R, T, U and W = urban high traffic sites. Abbreviations for study sites as well as values of air pollution levels are explained by STEINER (1994).

3.2 Classification of study sites

Classification of the eight study sites (where species analysis was performed) based on environmental characteristics (A), moss species (B), gaseous air pollutants (C) and fauna (D) is visualised in fig. 3. Environmental classification revealed two main clusters (fig. 3A), separating the rural sites "M" and "A" (cluster 2) from all the other sites (cluster 1). The final fusion is at a high similarity level, implying that the overall similarity among study sites is relatively high. When comparing this classification with inter-site relationships based on air quality alone (fig. 3C), it can be seen that clusters do not completely coincide. Thus, standardisation with respect to environmental characteristics other than pollution was appropriate.

Classification of study sites based exclusively on moss species (fig. 3B) showed within cluster 3 high floral similarity between the two sites with the highest traffic volume ("W" and "R"), and between the two rural sites "H" and "A", as well as between "O" and "M" (cluster 4). Inspection of the shaded similarity matrix shows that similarity between the sites "H" and "O" and between the sites "O" and "A" is greater than actually represented by the dendrogram.

Two clearly separated clusters (representing urban high traffic and rural sites) were detected when describing study sites by air pollution (fig. 3C). This classification is confirmed by statistical analysis, showing that the concentrations of each pollutant (i.e. SO_2, CO, NO and NO_2) differ significantly between the two urbanisation categories (Mann-Whitney U-test, $p < 0.05$). Air quality conditions are more uniform at the rural sites (cluster 6) than at urban sites (cluster 5). Site "H" is slightly separated, having an air quality similar to the urban site "U".

Classification of sites based on faunal composition (fig. 3D) revealed two clusters, corresponding to urban high traffic sites (cluster 7) and to rural sites (cluster 8), as detected in fig. 3C. Highest similarity values are observed between the urban sites "T" and "U", "W" and "U" (not represented in the diagram), as well as between "W" and "R". Faunal similarity between the rural sites was relatively low. This could be due to greater geographical distance as compared with urban sites, and/or to the more diverse fauna in rural moss cushions. The urban site "R" exhibits the smallest, and site "U" the highest similarity with the rural sites. The same situation was found when characterising study sites exclusively by air pollution (fig. 3C).

3.3 Classification of samples

The true relationships between samples may not necessarily correspond to groups based on geographical distances (i.e. to study sites) as considered so far. The classification and ordination of ecological communities represents an alternative approach to the analysis of samples pooled for each study site, as the inherent information of the samples is used. The classification of samples into distinct groups is based on $\hat{\tau}$ values using complete linkage clustering. Results of NMDS and cluster analysis are graphically combined in fig. 4. A hypothesised sample with uniform

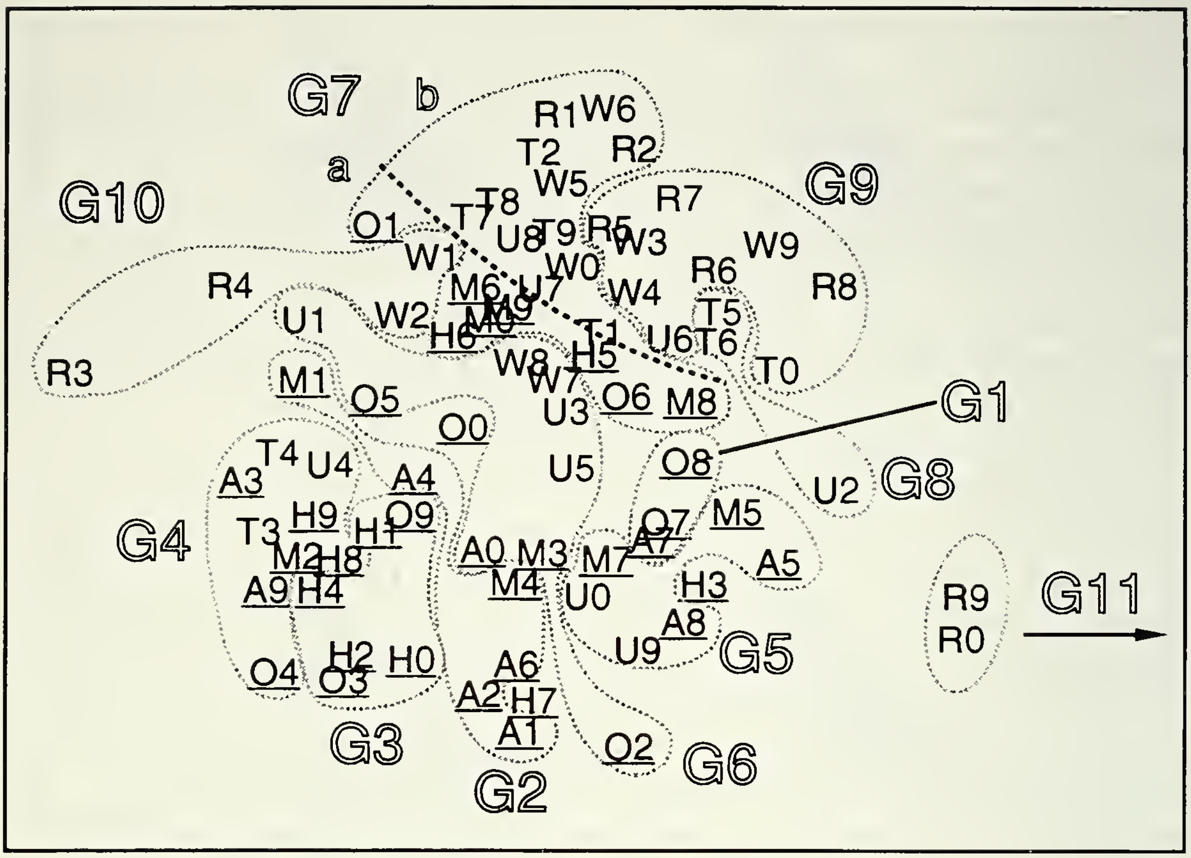

FIG. 4

Similarity map of the 80 samples in the survey of natural communities, obtained by nonmetric multi-dimensional scaling. Samples are characterised by moss-dwelling nematode and tardigrade taxa. The distances between all pairs of points reflect as closely as possible the measured similarity (τ index) of the corresponding samples. The classification of samples into groups is according to results of complete linkage clustering. A, H, M and O = rural low traffic sites (= underlined); R, T, U and W = urban high traffic sites; numbers 1 to 10 (= 0): sample numbers; G1 to G11: group identification. The samples O0 and H3 are members of G3. H7 is an isolated sample. The broken line in G7 separates rural from urban samples.

similarity to all the remaining samples is expected to be represented in the center, while samples characterised by a strongly divergent species composition would lie outside the bulk of the samples. In the present study R9 and R0 are outliers due to the unique presence of the predominant nematode species *Aphelenchoides* sp. 6. If this species is identical with *Aphelenchoides* sp. 4 (as supposed by STEINER, 1990), R9 and R0 would be located close to R7 and R8 (in G9). Samples taken from the same wall are usually represented as neighbouring points in the similarity plot (e.g. W1-W2 and R3-R4 in G10, T7-T8 and R1-R2 in G7b, etc.). This is confirmed by observations of preliminary studies (STEINER, 1990), which show that within a study site samples taken from the same wall are more similar than samples from different walls. For groups characterised by a wide-spread irregular shape on the NMDS similarity plot (e.g. G2 and G6) the group delimitation is rather artificial. On the other hand, some clusters show a good congruence between the two methods applied (e.g. G1, G4, and

G10). Thus, this classification is believed to have an ecological background rather than being an artefact of the underlying method.

Inspection of fig. 4 shows that faunal similarity of samples does not correspond to the study site level. For example, several urban samples (especially of site "U" in G5 and G6) show close similarity to rural samples, indicating that air pollution constitutes only a part of the environmental factors controlling the composition of nematode and tardigrade communities. If air pollution was the most important factor in determining the distribution and population sizes of species, the samples in the similarity map would be expected to fall into two well delimited clusters corresponding to the two air pollution categories revealed in fig. 3C. Thus, it may be of interest to search for the underlying structure, to describe it and to relate the observed similarities to environmental characteristics.

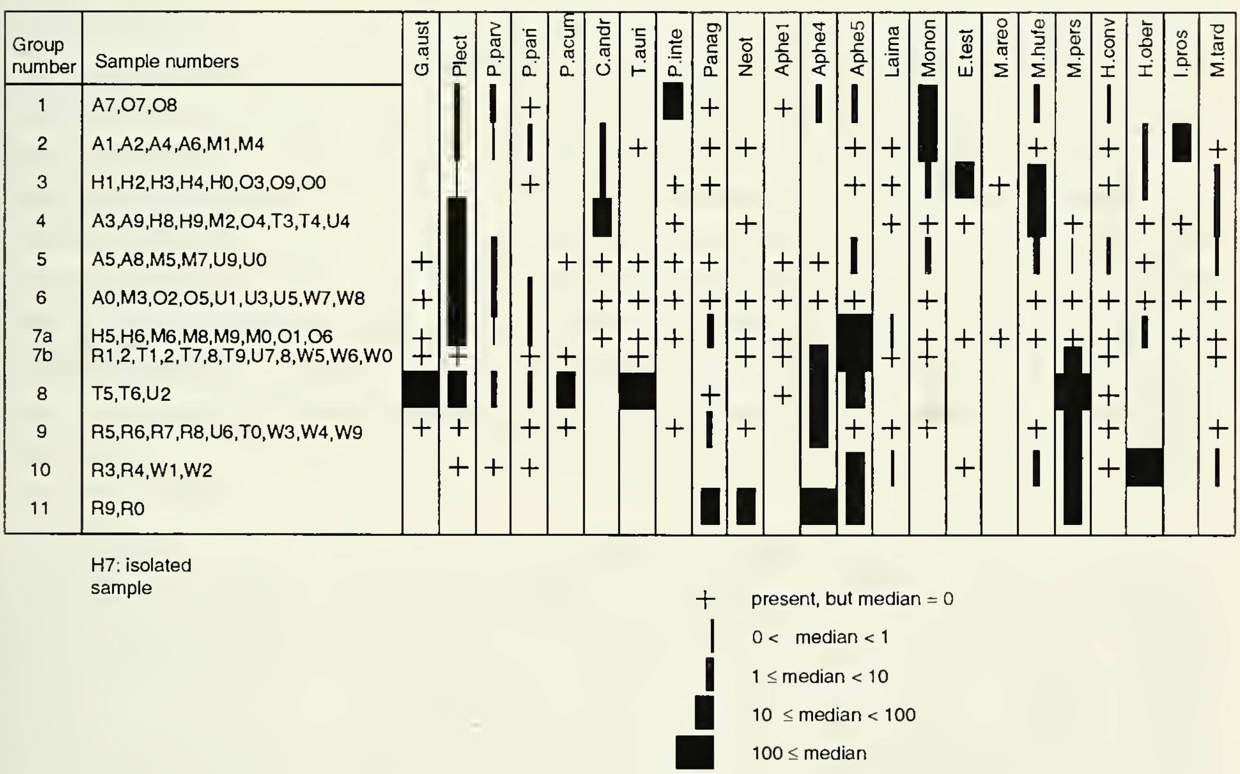

FIG. 5

Species composition of moss-dwelling nematodes and tardigrades (median/group) within groups of classified samples (i.e. 1 to 11, see fig. 4). H7 is an isolated sample; its composition is not represented. A, H, M and O = rural low traffic sites; R, T, U and W = urban high traffic sites. Abbreviations for species and study sites are explained in fig. 6 and by STEINER (1994a), respectively.

3.4 The search for indicator species

3.4.1 *Species composition within groups of classified samples*

Analysis of the faunal composition of sample groups G1 to G11 (fig . 4) provides information on ecologically similar taxa and helps define indicator species. In fig. 5, groups are arranged along the urbanisation gradient with G1, G2, G3 and G7a composed of rural samples only, while G7b to G11 consist exclusively of urban high traffic samples. Note that in G11 *Aphelenchoides* sp. 6 is replaced by *Aphelenchoides* sp. 4 (see Steiner, 1990) and could, therefore, be integrated into the closely related G9. The isolated rural sample H7 is strongly dominated by the predatory species *Milnesium tardigradum* Doyère and, to a lesser extent, by *Paratripyla intermedia* (Bütschli).

Mononchidae sp., *P. intermedia*, *Chiloplectus* cf. *andrassyi* (Timm), *Macrobiotus hufelandi* Schultze and *Isohypsibius prosostomus* Thulin are classified in groups with an overwhelming preponderance of rural samples (G1 to G5), whereas *Aphelenchoides* sp. 5, *Aphelenchoides* sp. 4 and *Macrobiotus persimilis* Binda & Pilato are typical of groups containing urban samples only (G7b to G11). The wide distribution of most species illustrates the presence of continually changing communities.

In addition to faunal similarity (fig. 5), some groups show common environmental characteristics. G1 to G3 are dominated by the moss species *Schistidium apocarpum* (Hedw.) and *Orthotrichum* sp., G7b, G9 and G11 by the toxitolerant *Bryum argenteum* Hedw. Furthermore, G1 and G3 contain only samples taken from sunken sandstone walls and from sunken or freestanding concrete walls, respectively. Mosses from groups with a majority of urban samples (i.e. G7b to G11) had a significantly higher pH (Mann-Whitney U-test, $p < 0.05$) than mosses from "rural" groups (i.e. G3 and G4). In contrast, both the size of moss cushions and the orientation of the wall seem to have no influence on group membership.

3.4.2 *Species assemblages*

The reason for examining the similarity between species is that interspecific associations are believed to be affected by environmental factors. Species often found together have ecologically similar requirements and could be used to indicate these conditions. The reordered similarity matrix and the associated diagram showing assemblages of species are represented in fig. 6. Highes $\hat{\tau}$ values are observed between *Dorylaimidae* sp. 2 and *Eudorylaimus* sp. 2, among the Neotylenchidae (species 1 to 4) and *Geomonhystera villosa* (Bütschli), as well as among *G. australis* (Cobb), *Plectus acuminatus* Bastian s.l. and *Tylocephalus auriculatus* (Bütschli). The high similarities among the different Neotylenchidae species confirm the hypothesis that these taxa are related (Steiner, 1990). The same is true for *C.* cf. *andrassyi* and Plectidae sp. (predominantly unidentified first larval instars). The discussion of species assemblages shown in fig. 6 will concentrate on assemblages consisting of relatively frequent species.

Assemblage 1 consists exclusively of tardigrade species. *Echiniscus testudo* (Doyère), *E. blumi* Richters and *Macrobiotus areolatus* Murray seem to be typical of dry habitats (Ramazzotti, 1972). The three species were frequently encountered in tegulous (living on tiles; from Latin: "tegula" = tile) mosses (Heinis, 1908b; Englisch, 1936; Steiner, 1994c).

The four members of assemblage 5, i.e. *Aphelenchoides* sp. 5, *Laimaphelenchus deconincki* Elmiligy & Geraert, *Hypsibius oberhaeuseri* (Doyère) and *M. tardigradum*, are widely distributed species (fig. 5). The two tardigrade species are known to associate in moss cushions all over the world (Richters, 1907; Heinis, 1908a; Englisch 1936; Morgan, 1977). *Hypsibius oberhaeuseri* and *Aphelenchoides* sp. 5 were also found to associate at the study site of long-term dynamics (Steiner, 1995b).

Assemblage 6 is composed of five nematode species. *Prionchulus muscorum* Dujardin predominates in rural samples, while the other species are more widely distributed (fig. 5). By inspection of the similarity matrix (fig. 6) evidence is drawn that *P. muscorum* could also be classified in species assemblage 8.

Assemblage 7 consists of species typical of urban areas, which are often accompanied by the ubiquitous species classified in species assemblage 5 (fig. 5). *Panagrolaimus* cf. *subelongatus* (Cobb) and *Aphelenchoides* sp. 4 reached maximum population sizes at the most polluted site "R". Maximum abundance of *M. persimilis* was recorded at site "W", which is characterised by the highest levels of SO_2 and CO (Steiner, 1994). Thus, species assemblage 7 is characteristic for polluted urban sites.

Members of assemblage 8 predominate in rural areas (fig. 5). Other than *Laimaphelenchus* sp. 1, species of this assemblage associate also in tegulous mosses (Steiner, 1995c).

Similarity coefficients between members of assemblage 9 are relatively high. This is based on two samples in which *P. acuminatus* s.l., *G. australis* and *T. auriculatus* were found in maximum numbers. Therefore, their similarity should not be overemphasised. In tegulous mosses, *T. auriculatus* was found to associate with *P. acuminatus* s.l. but also with the euryplastic species *Plectus* cf. *parietinus* Bastian (Steiner, 1995c).

The two remaining species assemblages 10 and 11 are difficult to interpret, since they comprise several composed taxa (see Steiner, 1994a). *Hypsibius convergens* Urbanowicz s.l. was the only taxon occurring at a high frequency (30%). Members of the two assemblages are generally very abundant and frequent in rural samples. The similarity values displayed for *Aphelenchoides* sp. 1, *H. convergens* s.l. and *Eumonhystera* sp. in fig. 6 indicate that the species assemblages 10 and 11 probably form a single assemblage, related to species assemblages 4 and 6.

3.4.3 *Distribution of single species in relation to air pollution*

Any indicator species of air pollution should either dominate in polluted or in unpolluted areas. Nematodes and tardigrades occurring preferentially under urban or rural conditions are thus potential candidates. Several taxa were found to reach significantly higher population densities either in urban or rural samples (tab. 3).

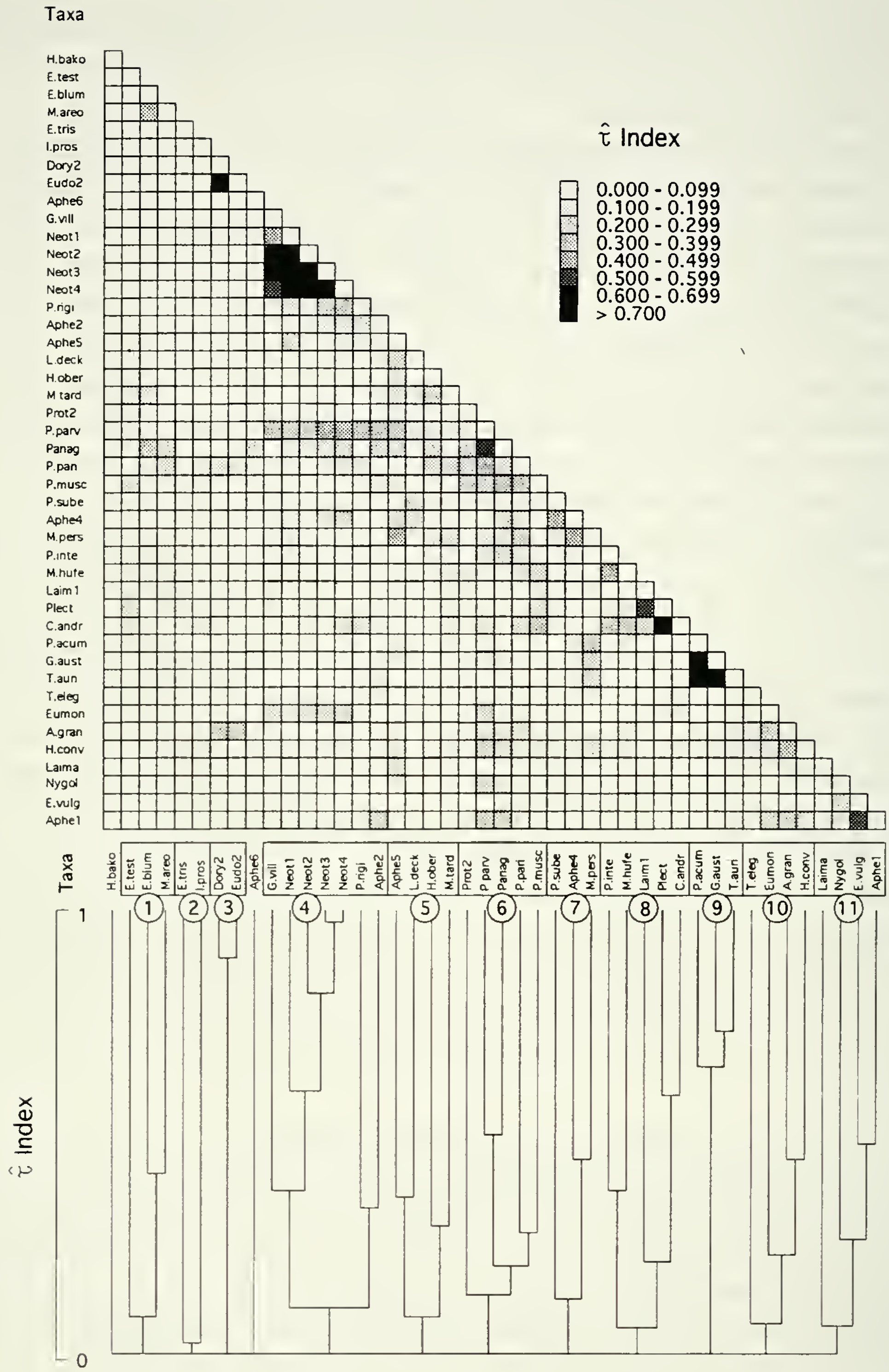

FIG. 6

Similarity matrix and dendrogram representing habitat overlap of 44 selected nematode and tardigrade taxa in the survey of natural communities. The similarity coefficients $\hat{\tau}$ are replaced by a shaded grid and rearranged by complete linkage cluster analysis to bring similar species to each other. Indicated species assemblages (rectangles with identification numbers) are discussed in the text.

TAB. 3

Differences in the distribution of nematode and tardigrade taxa among 40 urban and 40 rural samples (p: two-tail probability of the Mann-Whitney U-test, corrected for ties; Ranks: sum of ranks; u: urban; r: rural; NE: nematodes; TA: tardigrades).

Taxon		p	Ranks
NE	*Plectus acuminatus* s.l.	0.008	u > r
	Plectus parvus	0.016	u < r
	Plectidae sp. (larvae)	<0.001	u < r
	Chiloplectus cf. *andrassyi*	<0.001	u < r
	Aphelenchoides sp. 4	<0.001	u > r
	Aphelenchoides sp. 5	0.014	u > r
	Paratripyla intermedia	<0.001	u < r
	Mononchidae sp.	<0.001	u < r
TA	*Echiniscus testudo*	<0.001	u < r
	Macrobiotus hufelandi	0.003	u < r
	Macrobiotus persimilis	<0.001	u > r
	Hypsibius oberhaeuseri	<0.001	u < r
	Isohypsibis prosostomus	<0.001	u < r

Fig. 7 shows changes in the abundances of potential indicator taxa in a two-dimensional pollution gradient. The higher the air pollution levels are, the simpler and more uniform is the structure of the moss-dwelling community. Bacterial feeders (i.e. *C.* cf. *andrassyi*) and predators (*P. intermedia* and Mononchidae sp.) are dominant at rural sites, whereas fungal feeders (*Aphelenchoides* sp. 4 and 5) and *M. persimilis* (unknown feeding habits, probably a predator) yield higher populations under urban conditions. *Macrobiotus hufelandi* (omnivorous) is the only "rural" species present in noticeable numbers at urban sites too. At the most polluted sites "W" and "R", *M. hufelandi* becomes scarce and is replaced by its sibling species *M. persimilis*. This hypothesis is supported by findings of exposure experiments (STEINER, 1995c),

Abbreviations for taxa (in alphabetic order): A.gran: *Anaplectus granulosus*; Aphe1: *Aphelenchoides* sp. 1; Aphe2: *Aphelenchoides* sp. 2; Aphe4: *Aphelenchoides* sp. 4; Aphe5: *Aphelenchoides* sp. 5; Aphe6: *Aphelenchoides* sp. 6; C. andr: *Chiloplectus* cf. *andrassyi*; Dory2: Dorylaimidae sp. 2; E. blum: *Echiniscus blumi*; E. test: *Echiniscus testudo*; E. tris: *Echiniscus trisetosus*; E. vulg: *Eumonhystera vulgaris*; Eudo2: *Eudorylaimus* sp. 2; Eumon: *Eumonhystera* sp., G. aust: *Geomonhystera australis*; G. vill: *Geomonhystera villosa*; H. bako: *Hypsibius* cf. *bakonyiensis*; H. conv: *Hypsibius convergens* s.l.; H. ober: *Hypsibius oberhaeuseri*; I. pros: *Isohypsibius prosostomus*; L. deck: *Laimaphelenchus deconincki*; Laim1: *Laimaphelenchus* sp. 1 (group pannocaudatus); Laima: *Laimaphelenchus* sp.; M. areo: *Macrobiotus areolatus*; M. hufe: *Macrobiotus hufelandi*; M. pers: *Macrobiotus persimilis*; M. tard: *Milnesium tardigradum*; Neot1: Neotylenchidae sp. 1; Neot2: Neotylenchidae sp. 2; Neot3: Neotylenchidae sp. 3; Neot4: Neotylenchidae sp. 4; Nygol: *Nygolaimus* sp.; P. rigi: *Panagrolaimus* cf. *rigidus*; P. sube: *Panagrolaimus* cf. *subelongatus*; Panag: *Panagrolaimus* sp.; P. inte: *Paratripyla intermedia*; Plect: Plectidae sp.; P. acum: *Plectus acuminatus* s.l.; P. pari: *Piectus* cf. *parietinus*; P. parv: *Plectus parvus*; Plect: *Plectus*, larvae; P. musc: *Prionchulus muscorum*; Prot2: *Protorhabditis* sp. 2; T. eleg: *Tylenchus elegans- T. ritae*; and T. auri: *Tylocephalus auriculatus*.

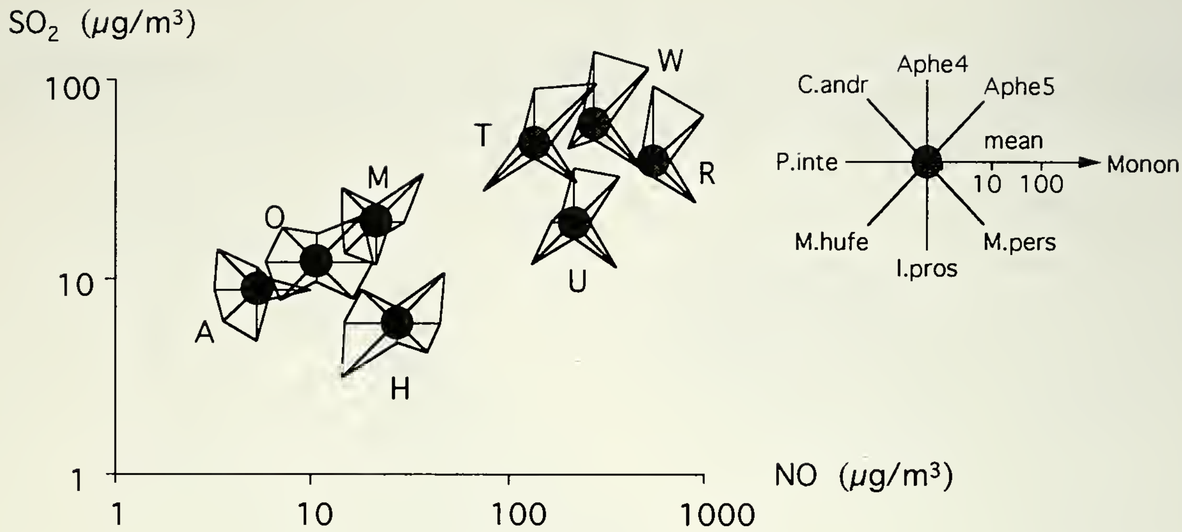

FIG. 7

Distribution of selected nematode and tardigrade taxa in a two-dimensional pollution gradient. Note that species abundances (arithmetical mean/site) and annual mean levels of SO_2 and NO have a log scale. The shaded circles delimit zero counts. Abbreviations for study sites as well as values of air pollution levels are explained by STEINER (1994a). Monon: Mononchidae sp., including *Prionchulus muscorum*; abbreviations for other species are explained in fig. 6; mean: log mean of species abundance.

showing that at the polluted sites *M. persimilis* invaded the moss cushions populated by *M. hufelandi* and got established there. Other species that probably respond sensitively to air pollution are *Plectus acuminatus* s.l., *P. parvus* Bastian, *E. testudo* and *H. oberhaeuseri* (tab. 3). In addition, *G. villosa* (in 5 samples), *Laimaphelenchus* sp. 1 (3), and *Panagrolaimus* cf. *rigidus* (Schneider) (5) are restricted exclusively to rural samples, while *P.* cf. *subelongatus* (5) was present only in urban samples.

Correlation analysis (tab. 4) confirms findings from the classification of samples (fig. 5) and the star-diagram (fig. 7). *Macrobiotus persimilis* and *Aphelenchoides* sp. 4 are toxitolerant species characteristic of heavily polluted roadside sites, whereas *P. intermedia* and *C.* cf. *andrassyi* are negatively correlated with both SO_2 and NO_2 levels. Additionally, *I. prosostomus* and Mononchidae sp. are negatively correlated with NO_2 pollution.

4 DISCUSSION

Community characteristics

Total abundance of any higher taxonomic category can easily be analysed. Reaching larger populations at the more polluted sites, nematodes can probably serve as an indicator for gaseous pollutants (fig. 2, tab. 2). More information, though, is provided by analysing communities at the species level than by working with

TAB. 4

Correlation of the abundances of nematode and tardigrade taxa with annual mean levels of SO_2 and NO_2 (SO_2 and NO_2 in µg/m^3; r_s: Spearman rank correlation coefficient corrected for ties; n = 8; p: tied probability).

Higher taxonomic category Species	r_s	p
Nematodes - SO_2		
Chiloplectus cf. *andrassyi*	- 0.86	0.024
Aphelenchoides sp. 4	+ 0.84	0.026
Paratripyla intermedia	- 0.97	0.010
Tardigrades - SO_2		
Macrobiotus persimilis	+ 0.76	0.046
Nematodes - NO_2		
Chiloplectus cf. *andrassyi*	- 0.89	0.018
Aphelenchoides sp. 4	+ 0.84	0.027
Paratripyla intermedia	- 0.85	0.025
Mononchidae sp.	- 0.80	0.035
Tardigrades - NO_2		
Macrobiotus persimilis	+ 0.78	0.039
Isohypsibius prosostomus	- 0.86	0.024

abundances of higher taxonomic categories. The most important changes with increasing pollution reflect simplification of tardigrade communities measured as a loss of species (fig. 1, tab. 2). The same response to pollution was found by HEINIS (1910), MATHEWS (1971), SÉMÉRIA (1981, 1982) and MEININGER & *al.* (1985) for moss-dwelling tardigrades. Thus, nematodes and tardigrades are potential indicators of air pollution, and it seems reasonable to discuss the sensitivity of the moss-dwelling aquatic fauna more in detail.

Classification and ordination of moss-dwelling communities were used to detect sample (and study site) groupings that reflect the abundances of the major species along the pollution gradient. Classification of study sites based on the aquatic fauna highly reproduced their similarities based on air pollutants, whereas different sites were combined into clusters when describing them by their flora or environmental variables (fig. 3). This, in turn, means that the moss-dwelling nematode and tardigrade fauna can be used to indicate air quality. The same conclusion was drawn by analysing the succession of aquatic species along the gradient of pollution at the sample level (fig. 5).

The low importance of moss species for the composition of the inhabiting fauna can be illustrated by comparison of the sites "A", "U" and "H". Although the sites "A" and "U" have a very similar flora (fig. 3B), their fauna differs considerably (fig. 3D). On the other hand, an inverse situation was found at the sites "U" and "H". The relatively high faunal similarity between "U" and "H" probably reflects their similarity in both environmental characteristics (fig. 3A) and air quality (fig. 3C).

Species assemblages and indicator species

Based on habitat overlap, several species assemblages could be delimited (fig. 6). These assemblages were generally loosely connected, corresponding to findings of DASTYCH (1980) for tardigrades. According to SOHLENIUS (1985), low species affinity is typical of unstable communities encountered in fluctuating environments and for taxa with a low degree of microhabitat specialisation such as nematodes. Two of the species assemblages detected were clearly related to pollution, being either characteristic for heavily polluted roadside ecosystems (fig. 6, assemblage 7) or for unpolluted rural areas (fig. 6, assemblage 8).

Three species (i.e. *Aphelenchoides* sp. 4, *Aphelenchoides* sp. 5, and *Macrobiotus persimilis*) are considered pollution tolerant, characterised by increasing populations from rural to urban roadside samples (fig. 5, tab. 4). In contrast, populations of *Chiloplectus* cf. *andrassyi*, *Paratripyla intermedia*, Mononchidae (cf. *Prionchulus muscorum*) and *Macrobiotus hufelandi* seem to be adversely affected by air pollution (fig. 5, tab. 4). Findings of fumigation and/or exposure experiments (STEINER, 1995c) confirm that most of these species could be used as indicators of air quality. At the polluted exposure sites *M. persimilis* invaded several moss cushions populated by *M. hufelandi* and got established there (STEINER, 1995c). This shows its ability to endure air pollution and its power of dispersal. *Aphelenchoides* sp. 4 was present at the most polluted site "R" in both natural (fig. 5) as well as in exposed moss cushions (STEINER, 1995c), whereas *C.* cf. *andrassyi* and *P. intermedia* were absent. The two nematode species were absent also in naturally growing moss cushions at the urban high traffic site "T" (figs. 5 and 7), but survived in moss cushions transplanted to the same site (STEINER, 1995c). Thus, findings for *C.* cf. *andrassyi* and *P. intermedia* did not completely coincide in the two approaches, probably due to the relatively short exposure period in the transplantation experiment. As the sensitivity of *C.* cf. *andrassyi* and *P. intermedia* to SO_2 is confirmed by findings of the fumigation experiments (STEINER, 1995c), their suitability as indicators of air quality is beyond question. The Mononchidae (Dorylaimina) are also of special interest because of the sensitivity of the Dorylaimina towards environmental stress (BASSUS, 1968; WASILEWSKA, 1979) and to lead content in the moss cushion (ZULLINI & PERETTI, 1986).

Factors affecting the distribution of moss-dwelling nematodes and tardigrades

The detection of changes in community structure along the urban gradient does not provide any understanding of the causality. Because of the interactions among air pollutants and between anthropogenic and natural variables it is difficult to define the role of any single factor. The mechanisms by which the aquatic fauna of urban roadside mosses was affected in the present study are unknown. However, the comparison with fumigation and exposure experiments (STEINER, 1995c) and with the literature can help to explain the role of air pollution as a factor affecting moss-dwelling nematodes and tardigrades.

Air pollution

SO_2, CO, NO_2 and NO are — along with hydrocarbons and methane — the quantitatively most important immissions in Switzerland (IMFANGER, 1987). In the present study, only SO_2 and NO_2 are generally discussed. They represent two main pollution sources (fuel oil in domestic heatings and cars, respectively) and adequately explained the relationships between community characteristics and air pollution (tab. 2). Moreover, SO_2 was used in fumigation experiments (STEINER, 1995c), and NO_2 was highly correlated with both NO and CO ($n = 12$, $P = 0.05$; NO_2-NO: $R^2 = 0.76$; NO_2-CO: $R^2 = 0.80$). Whether these gaseous pollutants or accompanying chemical compounds represent the relevant toxic component is unknown.

SO_2 is toxic for micro-organisms (BABICH & STOTZKY, 1974) and is being used since a long time as a preservative by food chemists. Little is known, though, about the response of the aquatic microfauna to SO_2. LEETHAM & *al.* (1982) found reduced populations of tardigrades and non-stylet bearing nematodes in SO_2 treated soil plots, while stylet bearing nematodes and Mononchidae as well as soil rotifers appeared unaffected. Fumigation experiments with SO_2 (STEINER, 1995c) showed that high SO_2 levels ($\approx 585\ \mu g/m^3$) lead to the elimination of most nematode (especially bacterial feeders such as *C.* cf. *andrassyi*) and tardigrade taxa. Moreover, the number of nematodes and rotifers decreased consistently with increasing SO_2 levels, whereas tardigrades reached largest populations at intermediate SO_2 concentrations (65 and 195 $\mu g/m^3$). Since pH of the fumigated moss cushions decreased significantly with increasing SO_2 (STEINER, 1995c), the acidic nature of the habitat may have determined the community structure. Taxon specific responses of nematodes to changes in pH were demonstrated by MORGAN & MACLEAN (1968), BRZESKI & DOWE (1969) and GADEA (1974). In the 80 samples of the faunistic survey, abundances of *M. persimilis*, *Aphelenchoides* sp. 4, *Aphelenchoides* sp. 5 and nematodes as a group increased with pH values of the mosses (Spearman-rank correlation, $p < 0.05$). On the other hand, abundances of *C.* cf. *andrassyi*, *P. intermedia*, Mononchidae sp., *Echiniscus testudo*, *M. hufelandi*, *Isohypsibius prosostomus*, and the number of tardigrade species decreased (Spearman-rank correlation, $p < 0.05$). The low number of tardigrade species at high pH values corresponds to findings of DASTYCH (1980). However, in the present study pH values of urban mosses were higher than those of rural mosses (Mann-Whitney U-test, $n = 80$, $p < 0.001$), although SO_2 levels were considerably higher at the urban sites (STEINER, 1994). These contradictory trends in pH shifts make an equivocal statement about the causes of SO_2 induced community changes impossible. Taking into account the almost complete absence of the bacterial feeding nematode *C.* cf. *andrassyi* in the fumigation experiments at pH values of four to five (STEINER, 1995c), as well as in urban roadside samples at pH values that ranged in the optimum for bacterial growth (CLARK, 1967), pollution appears more important for this species than the pH of the moss cushions.

No indications are found in the literature concerning effects of NO_x on moss-dwelling or soil-dwelling aquatic animals. Since NO_x is correlated with automotive emissions such as CO, ethylene and acetylene (KOPCZYNSKI & *al.*, 1975; GARNETT,

1979) as well as Pb (LAHMANN, 1979), heavy metals should be included in the discussion of faunal characteristics at urban high traffic sites. The uptake of airborne heavy metals by mosses (LITTLE & MARTIN, 1974; RASMUSSEN, 1977), bacteria (DOELMAN & *al.*, 1984) and fungi (PETERSEN & LUXTON, 1982) is well known, and will influence microbial degradation processes (BABICH & STOTZKY, 1974). In Zurich NO, NO_2, CO and Pb in suspended dust (BACHMANN-STEINER & *al.*, 1983), as well as Cu, Zn, Pb and Cd in moss cushions (SCHMID-GROB, 1984; THÖNI, 1984), is positively correlated with traffic volume. Urban roadside mosses are thus expected to have higher concentrations of heavy metals than mosses from rural or urban low traffic sites. Pb and Cd, when taken up by bacteria and fungi, have an inhibitory effect on the reproductive rate of fungal-feeding and bacterial-feeding nematodes (DOELMAN & *al.*, 1984). Moreover, Pb is reported to reduce the life-span (BAICHEVA & *al.*, 1980), species richness and diversity (POPOVICI, 1981; ZULLINI & PERETTI, 1986), biomass (ZULLINI & PERETTI, 1986), and population size (KOZLOWSKA, 1981; BISESSAR, 1982) of nematodes. Response of nematodes to copper is dose specific (PARMELEE & *al.*, 1993). At high concentrations of copper in soil (400 and 600 µg/g), nematode numbers were strongly reduced. However, at intermediate levels (100 and 200 µg/g), nematode populations increased as compared to the control, presumably due to the strong reduction of sensitive predatory nematodes. Such a mechanism could be involved in the increase of nematode numbers with increasing pollution, which parallels the decline in the abundance of predators such as Mononchidae sp. and *P. intermedia* (tab. 4).

Evidence exists that the influence of air pollution on the aquatic fauna is indirect via the food resource. As bacteria are usually more severely inhibited by pollution and/or acidification than fungi (BEWLEY & CAMPBELL, 1980; HÅGVAR & AMUNDSEN, 1981; DOELMAN & *al.*, 1984; KHANNA, 1986), pollution is expected to change the proportion of the trophic groups within moss-dwelling animal communities. Fungal-feeding nematodes predominated in heavily polluted roadside samples and bacterial-feeding nematodes in rural samples (chapter 3.4.3). A similar response of nematodes to heavy metal pollution was observed by BAICHEVA (1976), and to acidification by RATAJCZAK & *al.* (1989) and RUESS & *al.* (1993). Findings of exposure experiments (STEINER, 1995c) denote the important role of the microflora for moss-dwelling nematode communities. By exposing such communities together with the required microflora (within tegulous moss cushions), the aquatic fauna remained qualitatively unchanged at most study sites, i.e. bacteriophagous nematodes could survive at sites where natural communities were invariably dominated by mycophagous nematodes. Further evidence for an indirect effect of pollution on the aquatic fauna can be derived from a more theoretical point of view. According to ANDERSON & HALL (1977) and ANDERSON (1978), highly diverse communities develop as a function of high microhabitat diversity. Thus, the relatively simply structured communities observed at the high traffic sites (figs. 1, 2 and 7) could be a consequence of low microhabitat diversity (i.e. impoverished microflora), a hypothesis also suggested by MEININGER & *al.* (1985).

Influence of factors other than pollution

Although sampling was as uniform as possible (tab. 1), small variations in environmental factors (chapter 2.2) or different moss species might have influenced the faunal composition. However, environmental factors related to humidity conditions (i.e. type of wall, substratum, orientation of the wall) and abundances of common taxa or community characteristics were only loosely correlated. This is surprising considering the important role of moisture for the abundance of moss-dwelling nematodes (SMOLIK, 1982) and tardigrades (BERTRAND, 1975), as well as for the competitive ability of nematode species (SOHLENIUS, 1985).

The relatively weak dependence of moss-dwelling animals on definite moss species (chapter 3.4) agrees with findings for tardigrades (MARCUS, 1929; IHAROS, 1975; NELSON, 1975; DASTYCH, 1980; KATHMAN & CROSS, 1991) and nematodes (NIELSEN, 1948; RAMAZZOTTI, 1958; ZULLINI, 1975). Since the moss flora in roadside ecosystems and in rural areas was divergent, it is difficult to decide whether urban conditions act directly or indirectly (via the moss species) on the inhabiting fauna. Only samples of the widespread *Bryum argenteum*, allow us to check the influence of the moss species. Although the rural samples H5, H6, A1 and A2 (fig. 4) were all collected from *B. argenteum*, the two former (in G7a) are similar to urban samples, while the latter (in G2) are closely related to rural samples. Interestingly, H5 and H6 were taken from a parking place, and are, according to LÖTSCHERT & *al.* (1975), expected to have high levels of Pb. Differences in faunal composition, even within communities sampled from the same moss species at all sites, indicate thus that abiotic characteristics are more important for the aquatic fauna than the moss species itself. The same conclusions were drawn by analysis of the factors influencing faunal composition at the study site level (fig. 3).

Other topics

As several of the moss-dwelling species also occur in the soil (NIELSEN, 1948; NICHOLAS, 1975), soil-dwelling nematode communities of urban roadside sites in the city of Zurich are potentially influenced by the air quality. Although nematodes generally contribute less than 1% of the total soil respiration (YEATES, 1979), they interact with many other soil biota (CAYROL, 1976; WASILEWSKA & BIENKOWSKI, 1985). Microbial grazing and translocation of microbial inoculum (WIGGINS & CURL, 1979; VISSER, 1985) result in enhanced nutrient circulation (COLEMAN & *al.*, 1977, 1978; ANDERSON & *al.*, 1981) and eventually in a higher productivity (YEATES & COLEMAN, 1982). Saprophagous animals may also directly affect plant fitness by maintaining a dynamic nutrient pool.

The importance of tardigrades for soil processes is almost unknown (RAMAZZOTTI, 1972). In moss communities, however, they seem to play a similar role as nematodes. Their biomass, respiration, consumption, egestion, assimilation and production was of the same magnitude as values given for rotifers and nematodes (DAVIS, 1981).

5 CONCLUSIONS

Results of the present investigation show that various factors interrelated with the pollution gradient influence the qualitative and quantitative composition of the aquatic bryofauna. In accordance with MALCEVSCHI (1977) the microhabitat does not appear to act with decisive influence upon the aquatic fauna. Comparative ranking of the influence of factors on the moss-dwelling fauna shows pollution first, environmental characteristics (chapter 2.2) second, and moss species last. Mosses from heavily travelled roadside sites are characterised by a comparatively high density of nematodes and low species richness of tardigrades and, to a lesser extent, of nematodes. At a trophic level, there was a shift along the urbanisation gradient from bacterial feeding and predaceous nematodes in rural areas to fungal feeding nematodes in urban roadside ecosystems. Pollution may act either indirectly through inhibition of the microflora, or by its direct impact (toxicity) on moss-dwelling communities. At the species level, *Aphelenchoides* sp. 4, *Aphelenchoides* sp. 5 and *Macrobiotus persimilis* were characteristic for polluted mosses, while *Chiloplectus* cf. *andrassyi*, *Paratripyla intermedia* and *Prionchulus muscorum* typically occurred in rural mosses.

Changes in the biotic composition along the pollution gradient are considered to be a consequence of air pollution. Due to high similarity between the soil and moss fauna, pollution levels as encountered in the center of Zurich are also expected to change the structure of soil animal communities. Taking that the structure is closely related to the ecosystem function, these changes could affect normal soil fertility. Since the moss-dwelling aquatic fauna was sensitive to pollution and qualitatively stable over several years (STEINER, 1995b), it could be a convenient biological system for indicating levels of air pollution, and more important, a sensitive device for examining the ecological consequences of pollution on the soil biota.

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